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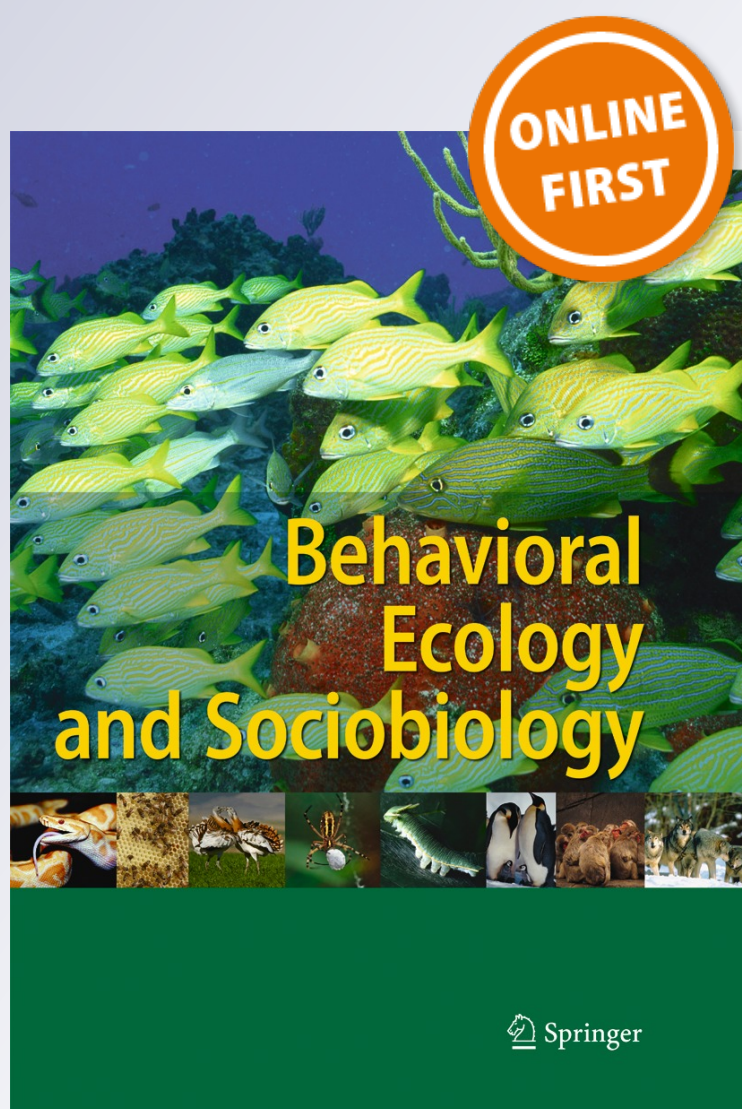
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Sea lamprey orient toward a source of a synthesized pheromone using odor-conditioned rheotaxis

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Abstract Characterization of vertebrate chemo-orientation strategies over long distances is difficult because it is often not feasible to conduct highly controlled hypothesis-based experiments in natural environments. To overcome the challenge, we couple in-stream behavioral observations of female sea lampreys (*Petromyzon marinus*) orienting to plumes of a synthesized mating pheromone, 7 α ,12 α ,24-trihydroxy-5 α -cholan-3-one-24-sulfate (3kPZS), and engineering algorithms to systematically test chemo-orientation hypotheses. In-stream field observations and simulated movements of female sea lampreys according to control algorithms support that

odor-conditioned rheotaxis is a component of the mechanism used to track plumes of 3kPZS over hundreds of meters in flowing water. Simulated movements of female sea lampreys do not support that rheotaxis or klinotaxis alone is sufficient to enable the movement patterns displayed by females in locating 3kPZS sources in the experimental stream. Odor-conditioned rheotaxis may not only be effective at small spatial scales as previous described in crustaceans, but may also be effectively used by fishes over hundreds of meters. These results may prove useful for developing management strategies for the control of invasive species that exploit the odor-conditioned tracking behavior and for developing biologically inspired navigation strategies for robotic fish.

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Introduction

Odorants mediate critical life history events of organisms, from unicellular bacteria to the largest vertebrates. Upon reception of an odorant, the receiver assesses the message in the context of its environment and behaves accordingly. Subsequently, the organism will often attempt to locate the odorant source. At the scales which bacteria or single eukaryotic cells operate, molecular diffusion of odorants can result in stable concentration gradients providing sufficient information to permit klinotaxis (concentration-based orientation; Dusenbery 1992). However, at macromolecule scales, turbulent flow of the transfer medium results in a highly intermittent chemical signal (Balkvosky and Shraiman 2002). In the atmosphere, unpredictable wind currents disperse pheromone signals through a three dimensional space resulting in highly intermittent bursts of pheromone only a few meters downwind (Murlis et al. 2000). In a salt marsh tidal creek, the constraints

of depth and width, along with typically unidirectional flow, result in reduced meandering of the odor plume, but the dynamic movement of water across uneven substrate still fragments the plume into intermittent filaments (Zimmer-Faust et al. 1995). In riverine systems, odor landscapes are similar to that of a salt marsh tidal creek and are more variable when large substrates are present (Moore et al. 2000).

To locate sources of turbulent odorant plumes, invertebrates and some fishes incorporate the olfactory input with visual cues and mechanical assessment of fluid flow (Hodgson and Mathewson 1971; Rittschof et al. 1983; Weissburg and Zimmer-Faust 1994; Gardiner and Atema 2007). Male moths use olfactory cues coupled with information on wind velocity and direction, determined by viewing the ground, to locate a female pheromone source (optomotor ammenotaxis; Kennedy and Marsh 1974; Murlis et al. 2000; Vickers 2000). Crustaceans, such as the lobster (*Homarus americanus*), blue crab (*Callinectes sapidus*), and rock crab (*Cancer irroratus*), use mechanoreceptors to determine flow direction and move upstream when an odorant is detected (odor-conditioned rheotaxis; also termed odor-gated rheotaxis; Moore et al. 1991), and use chemotaxis to inform fine scale cross-current movements by comparing concentrations across their bilateral sensory organs (chemotropotactic orientation; Page et al. 2011). Laboratory flume experiments show that orientation to food odorants in fishes is also governed by odor-conditioned rheotaxis in species such as the banded kokopu (*Galaxias fasciatus*), eels (*Anguilla rostrata*, *Anguilla australis*, *Anguilla dieffenbachii*), and smooth dogfish shark (*Mustelus canis*) (Oliver et al. 1996; Baker et al. 2002; Carton and Montgomery 2003; Gardiner and Atema 2007). Adult salmonids are hypothesized to navigate to natal streams using the remnants of river plumes in ocean microstructure layers by integrating odor-conditioned rheotaxis and infrasonic hearing (Doving and Stabell 2003). Data are limited, however, concerning movement patterns of fishes or other vertebrates to odorant plumes over distances of 10 m in natural environments and when data are available, they have been generally insufficient to unequivocally test chemo-orientation hypotheses (Westerberg 1982; Nevitt et al. 2008; Johnson et al. 2009).

The sea lamprey (*Petromyzon marinus*) is a well-suited organism to test fish chemo-orientation hypotheses in natural environments over biologically relevant distances. In their terminal life stage, sea lamprey use odorants released by larval sea lamprey to locate spawning streams (Sorensen et al. 2005; Vrieze et al. 2011) and mature males signal to mature females over 100 s of m the location of their nest by the release of a potent pheromone, 7 α ,12 α ,24-trihydroxy-5 α -cholan-3-one-24-sulfate (3kPZS; Li et al. 2002; Siefkes et al. 2005; Johnson et al. 2009). Female sea lampreys locate 3kPZS sources efficiently, even though they possess only a single olfactory organ in a nostril located in the centre of the head and thus cannot

use chemotropotaxis (Kleerekoper 1972). Moreover, two additional impediments, slow sampling rates of odorants and rapid movement through water current, likely limit lamprey's ability to resolve local concentrations (Weissburg 2000; Webster and Weissburg 2001; Webster and Weissburg 2009). Sea lamprey, having to rely on respiratory muscles to move water into and out of the nostril, can only sample the plume at low frequencies (Kleerekoper and Sibakin 1956). This sampling rate may be too slow to obtain reliable measurements of the dynamic properties of odor packets in a plume, such as concentration slope, peak or duration. Furthermore, the combined speed of their upstream movement, along with the downstream movement of water, is likely too fast for obtaining accurate time-averaged concentration estimates (Weissburg 2000; Webster and Weissburg 2001; Webster and Weissburg 2009). Mature female sea lamprey do not feed and do not use vision during upstream migration (Applegate 1950; Binder and McDonald 2007), and thus may focus all their swimming effort to tracking 3kPZS plumes with olfaction and mechanoreception. Synthesized 3kPZS is available for testing in natural streams, which is a distinct advantage to other vertebrate models for chemo-orientation, where the composition and concentrations of the active ingredients were largely unknown (Carton and Montgomery 2003; Gardiner and Atema 2007).

Previous field studies have clearly demonstrated that odorants function in the completion of critical life history events in fishes (Scholz et al. 1975), but determination of a vertebrate chemo-orientation strategy over biologically relevant distances has been difficult because it is often not feasible to conduct highly controlled hypothesis-based experiments in natural environments (Johnson and Li 2010). A potentially efficient strategy to characterize the movement patterns of sea lamprey in response to synthesized 3kPZS is through the coupling of in-stream observations and model-based algorithms to systematically exclude chemo-orientation hypotheses. Engineers often generate control algorithms that predict movements of organisms as they orient toward a source of pheromones, but rarely have data from natural systems by which to test the performance of their algorithms (Grasso et al. 1997, 2000; Li et al. 2001; Grasso and Atema 2002; Pang and Farrell 2006; Jatmiko et al. 2008). The proposed strategy will mutually benefit behavioral ecology and engineering by providing the biologist with feasible tests of orientation hypotheses and the engineer with physical and behavioral data to test search algorithms (Weissburg and Dusenbery 2002).

We hypothesize that female sea lampreys use a simple orientation mechanism, such as odor-conditioned rheotaxis, to locate a source of 3kPZS in turbulent flow given the biological characteristics of their olfactory system. Our objectives were to (1) characterize 3kPZS plumes in natural streams and describe female sea lamprey movement patterns

in relation to 3kPZS plumes and 2) couple observed sea lamprey behavior and physical data to test chemo-orientation hypotheses through algorithm-based approaches. Control algorithms were developed according to three orientation hypotheses: (1) rheotaxis, (2) odor-conditioned rheotaxis, and (3) klinotaxis. Each control algorithm was applied to physical observations of plume structure and stream flow to generate movement tracks of hypothetical sea lampreys. The simulated movement of sea lampreys in the natural stream produced by each algorithm was compared to observed movements of sea lampreys. The algorithm that best reflected observed data was then verified with sea lamprey behavior observed in a novel section of the same stream under four treatments: (1) flow with 3kPZS application, (2) flow with control solvent application, (3) reduced-flow with 3kPZS application, and (4) reduced-flow with control solvent application. Behavioral observations and simulated results from hypothesis-based control algorithms unequivocally show that sea lamprey must incorporate flow direction into their chemo-orientation strategy to successfully track 3kPZS plumes over hundreds of meters.

Methods

Synthesized 3kPZS, permits, and animals

Pre-ovulatory female sea lampreys were captured in mechanical traps fished in tributaries to Lakes Michigan and Huron. To facilitate sexual maturation, pre-ovulatory female sea lampreys were stocked in 1-m³ holding cages in the Ocqueoc and Black Mallard Rivers (Millersburg, MI, USA). A female was termed ovulated if eggs could be expressed with manual pressure to the abdomen. At least 24 h prior to experimentation, ovulated females were externally tagged with a 23 mm glass encapsulated passive integrated transponder (PIT tag; Oregon RFID, Portland, OR, USA) and two-color floy tags (Hallprint, Victor Harbor, South Australia) to facilitate visual observation during experimentation (Johnson et al. 2009). At least 12 h prior to experimentation, tagged ovulated females were transported to the experimental stream and placed in a 1-m³ release cage to acclimate. Additional details are provided in the [Online Resource](#).

Orientation of female sea lampreys to plumes of 3kPZS emanating from bifurcated stream channel

Test system

To characterize 3kPZS plume structure and female movements in relation to 3kPZS plumes, experiments were conducted in the bifurcated stream segment in the Ocqueoc River, Michigan, USA, described by Johnson et al. (2009).

Briefly, an island naturally divides the stream into two channels with similar discharge and velocity at their confluence (see Fig. S1). Synthesized 3kPZS was applied in each channel 45 m upstream of their confluence to produce an in-stream concentration of 5×10^{-13} M when fully mixed with discharge from both channels. Natural concentrations 3kPZS in sea lamprey spawning streams vary between 8.5×10^{-14} and 5×10^{-12} M during the spawning season (Xi et al. 2011). The application rate of 3kPZS in this bifurcated stream has been validated with a quantitative method (Xi et al. 2011). The bifurcated stream channel was a dynamic system in which sea lamprey would encounter a convergence of 3kPZS-activated flows from both channels allowing tracks of sea lamprey movement patterns to be examined in more versatile scenarios. Females will swim directly to the source of 3kPZS when only one of the two channels is baited (Johnson et al. 2009).

The female release cage was located 250 m downstream of the pheromone application locations. Visual observations of female movement patterns began 110 m downstream of the 3kPZS sources (Fig. S2). A PIT antenna system with multiplexer (Oregon RFID, Portland, OR, USA) recorded the number of females that entered each stream channel and located each 3kPZS source. Cross channel antennas were located 1 m upstream of the confluence of the left and right channels (referenced looking upstream). One m² antennas were placed around the 3kPZS application locations (see Fig. S1).

Procedures

Between June 2, 2007 and June 28, 2007, 15 trials were conducted. Between four and 12 ovulated females were released per trial. Since the sea lamprey spawning-phase is the terminal life stage, availability of ovulated females was limited and varied through time. A total of 144 ovulated female sea lampreys were released when 3kPZS 5×10^{-13} M was applied to the left and right stream channels. 3kPZS was applied from the release locations for 1 h prior to release and females were observed for 3 h after release. The amount of synthesized 3kPZS required for an experiment was dissolved in 1 ml methanol, mixed with 40 l river water, and applied to the stream at a rate of 167 ml/min via peristaltic pump (Masterflex 7553-70; Cole-Parmer, Vernon Hills, IL, USA) through a 4.8-mm (inside diameter) tube (Tygon R-3603; Cole-Parmer) over a 4-h application period (Johnson et al. 2009). Movement tracks of individual sea lamprey were manually observed and recorded on a map of the stream. When documenting the movement of a sea lamprey, a person would communicate the position of the sea lamprey to another person who recorded it on a stream map (see [Online Resource](#)). Previous studies show that behaviors of individual females are independent when released in groups (Johnson et al. 2005; Siefkes et al. 2005; Johnson et al.

2006, 2009). Specifically, the field experiments were conducted in the same stream, under similar conditions, as described by Siefkes et al. (2005), which provided a detailed treatment on the statistical analyses demonstrating independence of subjects.

3kPZS plume structure, water velocity mapping, and female movement track overlay

Rhodamine dye (Turner Designs, Rhodamine WT, Sunnyvale, CA, USA) tests were conducted to trace 3kPZS dilution and distribution in experimental test systems. Immediately after dye tests, depth and water velocity was determined at each dye sampling location using a Marsh McBirney Flow Mate 2000 flow meter with wading rod (Hach Company, Frederick, MA, USA). Methods to map the 3kPZS plume structure, velocity profile, and female movements were conducted as described by Johnson et al. (2009) (see [Online Resource](#)).

Fitting control algorithms based on orientation hypotheses to observed data

The fundamental rules of each hypothesis-based algorithm were founded on sea lamprey biology and the dynamic nature of turbulent flow. Sea lamprey sample the chemical environment through the tidal flow of water in and out of the olfactory epithelium every few hertz (Kleerekoper and Sibakin 1956; Kleerekoper 1972). For each sniff, the sea lamprey olfactory system takes a noisy measurement of the pheromone concentration c

$$z(k) = c(k) + w_s(k), \quad (1)$$

where k is the discrete time index. w_s is the measurement noise modeled by the Gaussian white noise $w_s(t_k) \sim N(0, \sigma_s^2)$ (Chang et al. 1998). A sampling time of 0.5 s was chosen for the discrete-time control algorithms for lampreys. This value for the sampling time was determined by the period of the sea lamprey's inhalation (Kleerekoper and Sibakin 1956) since in every inhalation, the sea lamprey takes new measurement. The discrete-time control algorithms can be viewed as sample-data systems based on sampling of the measurement (1). All control algorithms incorporate an obstacle avoidance capability as the highest priority to allow sea lamprey to stay in the river channel.

The control algorithms regulate the heading angle θ of the sea lamprey while keeping the forward velocity constant to direct it toward the 3kPZS source. The decision for θ depends on one of three factors: 3kPZS concentration (odor-conditioned rheotaxis and klinotaxis), flow velocity

(rheotaxis and odor-conditioned rheotaxis), and obstacles (all control algorithms).

Taking into account the fundamental algorithm rules described above, specific discrete-time kinematic models of sea lamprey chemo-orientation were developed, which can be considered as an averaged or sampled kinematic model of the sea lamprey. Pseudo-code and flowchart for each control algorithm is detailed in Figs. S3, S4, and S5. Computer simulations of each algorithm are available online. The model algorithms are as follows:

- (1) Rheotaxis: The sea lamprey moves upstream when it perceives flow greater than 0.05 m/s regardless of reception of 3kPZS or lack thereof.
- (2) Odor-conditioned rheotaxis: The sea lamprey moves upstream when it perceives flow greater than 0.05 m/s (rheotaxis; Montgomery et al. 1997; Kanter and Coombs 2003) and when it detects 3kPZS at or above a concentration threshold (i.e., when it is within the odor plume). Otherwise it executes a counterturning maneuver and is allowed to swim downstream if necessary to reacquire the odor plume. Movements are made with respect to flow direction.
- (3) Klinotaxis: The sea lamprey swims in the direction of increasing 3kPZS concentration without reference to flow direction. If the 3kPZS concentration does not increase, the sea lamprey randomly explores a new direction.

The three control algorithms were applied to spatial maps of 3kPZS concentration and water velocity observed in the bifurcated stream segment. Spatial maps of 3kPZS and water velocity vectors were obtained by smoothly interpolating the experimentally obtained discrete spatial data samples. Velocity data were measured in meters per second and the velocity vector field was inferred from the shape of the channel. Hence, in the simulation, 3kPZS and water velocity vectors for any given point were obtained by the reconstructed spatial fields of 3kPZS and water velocity vectors.

Determination of the best fit control algorithm in bifurcated stream

The number of simulated sea lampreys that entered the right and left channel and successfully located the 3kPZS source in each channel according to algorithms 1, 2, and 3 were compared to observed data. Significant differences between the overall distribution of sea lampreys simulated by algorithms 1, 2, and 3, and those observed were determined by logistic regression models, where the independent variable was the algorithm applied and dependent variable was the distribution of sea lampreys. Statistical results reported are from two-tailed analyses conducted in *R* (R Development Core Team 2009).

Furthermore, fine-scale movement patterns of simulated and of observed sea lampreys were compared using a performance cost function J (2),

$$J = \frac{|\sigma_{X_O} - \sigma_{X_S}|}{\sigma_{x_{st}}} + \frac{|\sigma_{Y_O} - \sigma_{Y_S}|}{\sigma_{y_{st}}} + \frac{|\bar{X}_O - \bar{X}_S|}{\bar{x}_{st}} + \frac{|\bar{Y}_O - \bar{Y}_S|}{\bar{y}_{st}} + (1 - \rho_{X_O, X_S}) + (1 - \rho_{Y_O, Y_S}) \quad (2)$$

where X_O , Y_O , X_S , Y_S are random variables that denote the x - and y -components of the observed trajectories and the x - and y -components of the simulated trajectories, respectively. Let \bar{X} , σ_X and $\rho_{X,Y}$ denote, respectively, the mean value of X , the standard deviation of X , and the correlation of X and Y (Myers and Well 2002). By the definition in Eq. 2, we obtain $J=0$ if the standard deviations σ and the means of two trajectories are the same, and $\rho_{X_O, X_S} = \rho_{Y_O, Y_S} = 1$ (Myers and Well 2002). However, since ρ is a non-dimensional quantity, the following variables are used to non-dimensionalize the standard deviations and means: x_{st} , y_{st} , where x_{st} and y_{st} are the horizontal and vertical lengths of the stream, respectively. Therefore, two trajectories are similar in a statistical sense (in terms of the first- and second-order moments) if they minimize J . Experimental trajectories were observed at non-uniform sampling times (see [Online Resources](#)). For a fair comparison, trajectory points of the observed data are interpolated to make their sampling time uniform and equivalent to the sampling time in simulated movements. In the bifurcated stream environment, the evaluation of J has been carried out locally over a partition of the stream in vertical segments to deal with the curvy bifurcated stream (Abarbanel et al. 1993). These local evaluations of J were then averaged to obtain the global cost. The mean and standard deviation of J after 20 simulations from each algorithm was calculated (one simulation = all sea lampreys observed in that treatment simulated). ANOVA was used to determine if the mean J from each algorithm differed significantly.

Movement patterns of female sea lampreys in response to 3kPZS in a novel test system to validate modeling results

To determine the robustness of best fitting control algorithm for sea lamprey movement patterns observed in the bifurcated stream, we also compared observed and simulated movement patterns of females to plumes of 3kPZS in a novel stream segment where mean water velocity could be reduced from 0.75 to nearly 0 m/s (Fig. S6). We reasoned that if the best fit algorithm effectively modeled sea lamprey chemo-orientation under diverse conditions, then when applied to novel test environments, simulated movements by the algorithm should still mimic those of sea lamprey.

Experiments were conducted in the Ocqueoc River in a similar bifurcated section as the first experiment. However, stream discharge under normal conditions was split approximately 90:10 between the two channels. The minor channel was used for behavioral experiments and was 25 m long. The amount of water flowing through the minor channel was regulated with a sandbag wing-dam. During flow condition experiments, the wing-dam was positioned to divert water from the major channel into the minor channel to increase water velocity. During reduced-flow condition experiments, the wing-dam was repositioned to prevent water from entering the minor channel.

Experiments were conducted under four conditions: (1) flow with 3kPZS application, (2) flow with control solvent application, (3) reduced-flow with 3kPZS application, and (4) reduced-flow with control solvent application. Behavioral response variables included whether the individual left the release cage, moved upstream, entered the 3kPZS-baited nest, or swam upstream past the baited nest. Variation in response variables among treatments was evaluated with logistic regression and models showed no evidence of over-dispersion or nonlinearities. Furthermore, the “best-fit” algorithm was applied to the novel experimental system under the four conditions above. The algorithm parameters calibrated in the bifurcated stream were used. The performance cost function (equation 2) was used to compare simulated sea lamprey movements by the algorithm to observed sea lamprey movements. Detailed procedures and plume mapping methods can be found in the [Online Resource](#).

Results

Behavioral responses of female sea lampreys to plumes of 3kPZS emanating from bifurcated stream

Forty-three females moved upstream and entered the bifurcated stream section (Table 1), which is a similar proportion as observed by Johnson et al. (2009). Females that did not enter the bifurcated stream section moved downstream or did not leave the release cage. Fifteen females entered the left channel and 28 females entered the right channel. Thirteen of the 15 females that entered the left channel also entered within 0.5 m of the left channel 3kPZS source. Twenty-six of the 28 females that entered the right channel also entered within 0.5 m of the right channel 3kPZS source. We recorded movement tracks from all the females that located the left 3kPZS source ($n=13$) and only 20 of the 26 females that located the right 3kPZS source due to more difficult observation conditions. Most sea lampreys that located a 3kPZS source moved directly upstream with few sidestream or downstream deviations greater than 1 m

Table 1 Algorithm modeling odor-conditioned rheotaxis simulated large-scale chemo-orientation patterns of ovulated female sea lampreys to plumes of 3kPZS

Data source	Observed (<i>n</i>)	Left channel (<i>n</i>)	Right channel (<i>n</i>)	% Success left (<i>n</i>)	% Success right (<i>n</i>)
Experimental	33	13 a	20 a	92 % a	95 % a
Rheotaxis	33	22 b	11 b	41 % b	0 % c
O-C rheotaxis	33	16 a	17 a	88 % a	82 % b
Klinotaxis	33	3 c	10 c	0 % na	0 % na
<i>p</i>	NA	<0.001	Same as left channel	<0.001	<0.001
<i>df</i>	NA	3		2	2
χ^2	NA	32.16		37.86	40.25

Observed (*n*) is the number of ovulated female sea lampreys for which full movement tracks were recorded in the bifurcated stream channel when synthesized 3kPZS was applied simultaneously to both channels (experimental), and the number of simulated females according to algorithms modeling rheotaxis, odor-conditioned rheotaxis (O-C rheotaxis), and klinotaxis. Percent success left and right is the percent of the sea lampreys that entered the left or right channel that also entered within 0.5 m of the left 3kPZS source or right 3kPZS source. Significant differences between treatments determined with generalized linear model assuming a binomial family. Treatments with the same letter are not significantly different ($\alpha=0.05$).

NA not applicable

(Fig. 1a). Water velocity in the stream channel varied from 1.1 to 0.0 m/s (Fig. S1).

Model predicted movement patterns of female sea lampreys to plumes of 3kPZS emanating from bifurcated stream

The algorithm modeling odor-conditioned rheotaxis (algorithm 2) produced simulated sea lampreys whose macro-scale movements into the left and right channel were not different than female sea lampreys tracking plumes of 3kPZS ($t=-0.254$, $df=128$, $p=0.800$; Table 1). The efficiency of control algorithm 2 simulated lampreys that entered the left channel to locate the 3kPZS source was not different than female sea lampreys ($t=-0.675$, $df=43$, $p=0.500$; Table 1). When considering movements in the right channel, the efficiency of control algorithm 2 simulated sea lampreys to locate the 3kPZS source was less than female sea lampreys (right channel: $t=-2.379$, $df=60$, $p=0.017$), but greater than control algorithms modeling rheotaxis (algorithm 1) and klinotaxis (algorithm 3). Control algorithms 1 and 3 produced simulated sea lampreys whose movements into the left and right channel were significantly different from female sea lampreys tracking plumes of 3kPZS (algorithm 1: $t=1.950$, $df=128$, $p=0.050$; algorithm 3: $t=-2.820$, $df=128$, $p=0.005$; Table 1). Logistic regression models showed no evidence of overdispersion.

Control algorithm 2 produced simulated micro-scale movement trajectories that were similar to those displayed by female sea lamprey tracking plumes of 3kPZS (Fig. 1). Performance cost function of algorithm 2 was low and significantly less than algorithms 1 and 3 ($t=5.90$, $df=57$, $p<0.001$; $t=20.20$, $df=57$, $p<0.001$; Table 2), demonstrating that algorithm 2 best described the movement patterns of ovulated female sea lampreys in the bifurcated stream.

Behavioral responses of female sea lampreys to a source of 3kPZS and control solvent in flow and reduced-flow environments

When exposed to 3kPZS in flow conditions (Fig. S6; 0.75 m/s at 5 m mark), a greater percentage of ovulated females left the release cage, moved upstream, and entered the 3kPZS-baited nest than when control solvent was applied under flow conditions (Table 3 and Fig. 2; leave release cage: $t=-2.973$, $df=200$, $p=0.003$; move upstream: $t=-4.491$, $df=200$, $p<0.001$; enter nest: $t=-3.634$, $df=200$, $p<0.001$) and reduced-flow conditions (leave release cage: $t=-1.984$, $df=200$, $p=0.047$; move upstream: $t=-4.986$, $df=200$, $p<0.001$; enter nest: $t=-3.901$, $df=200$, $p<0.001$). When females were exposed to 3kPZS in reduced-flow conditions (Fig. S6; 0.05 m/s at 5 m mark), a greater percentage of ovulated females moved upstream than when control solvent was applied under flow conditions ($t=-2.240$, $df=200$, $p=0.025$) and reduced-flow conditions ($t=-3.086$, $df=200$, $p=0.002$). However, more females swam past the odorant-source without locating the nest when exposed to 3kPZS in reduced-flow conditions than when exposed to 3kPZS in flow conditions ($t=-2.098$, $df=200$, $p=0.036$). The percent of females locating the nest when 3kPZS was applied under reduced-flow conditions was less than when 3kPZS was applied under flow conditions ($t=3.485$, $df=200$, $p<0.001$), and not different than when control solvent was applied under flow conditions ($t=-1.039$, $df=200$, $p=0.180$) and reduced-flow conditions ($t=-1.756$, $df=200$, $p=0.079$).

Control algorithm 2 was applied to the four treatment data sets described above to evaluate its performance in physical habitats that were not used for calibrating it. Simulated movements of sea lampreys by algorithm 2 in flow

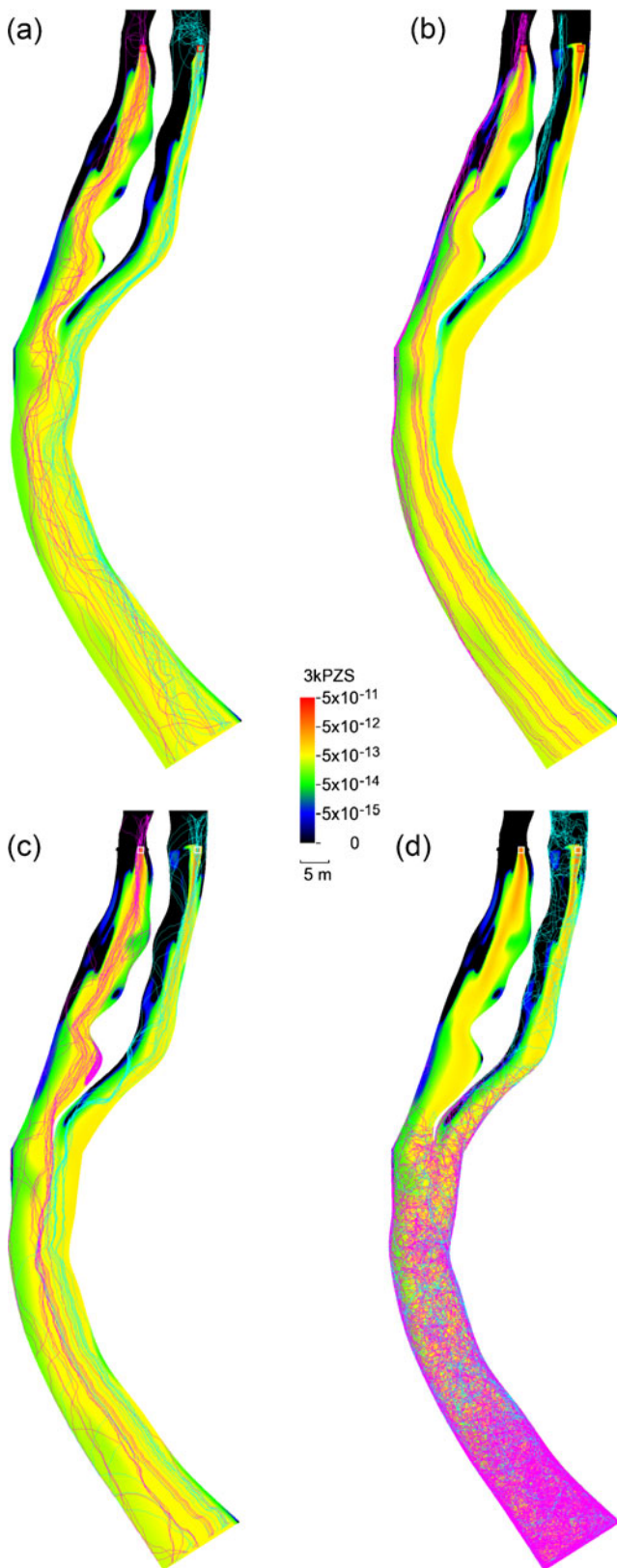


Fig. 1 Algorithm modeling odor-conditioned rheotaxis best replicates chemo-orientation of sea lampreys tracking plumes of synthesized 3kPZS in natural stream. **a** Observed movement tracks of ovulated female sea lampreys that moved into a channel of the bifurcated stream channel. Modeled movement tracks of ovulated female sea lampreys according to algorithms 1 (rheotaxis, **b**), 2 (odor-conditioned rheotaxis, **c**), and 3 (klinotaxis, **d**). Red tracks are the females that entered the left channel and blue tracks are the females that entered the right channel. Color shading indicates the estimated molar concentration of synthesized 3kPZS through the stream channel. White boxes indicate the location of the 3kPZS sources

with 3kPZS application was significantly higher than simulations in the bifurcated stream (Table 4; J of algorithm 2 in bifurcated stream = 2.32 verse J of algorithm 2 in flow — 3kPZS condition = 3.17; $t = -7.51$, $df = 38$, $p < 0.001$), suggesting a poorer fit to observed data in the novel test system. Movement tracks of sea lampreys according to algorithm 2 in flow conditions with control solvent application, reduced-flow conditions with 3kPZS application, and reduced-flow conditions with control solvent application resemble the non-targeted random movement patterns of sea lampreys in these environments (Fig. 3).

Discussion

In-stream field observations of female sea lamprey movement patterns strongly support that odor-conditioned rheotaxis is a component of the chemo-orientation strategy used to track plumes of 3kPZS over long distances in rivers. In the bifurcated stream, the straight upstream movement trajectories of observed sea lampreys support the hypothesis that mean flow direction is critical for sea lamprey to track 3kPZS plumes. Observations of female movement patterns to plumes of 3kPZS in flow and reduced-flow conditions systematically confirmed observations of odor-conditioned rheotaxis in the bifurcated stream channel. When exposed to a plume of 3kPZS in flow conditions, female movement trajectories were straight upstream, with high rates of

conditions with 3kPZS application resemble observed sea lamprey movements (Fig. 3). However, the performance cost function of sea lamprey movement in flow conditions

Table 2 Algorithm modeling odor-conditioned rheotaxis best simulated fine-scale movement patterns of sea lampreys in bifurcated stream channel emanating plumes of 3kPZS

Control algorithm	\bar{J}	σ_J
Rheotaxis	3.1165 b	0.3232
O-C rheotaxis	2.3203 a	0.3485
Klinotaxis	5.0479 c	0.5666

\bar{J} and σ_J are the mean and standard deviation of the performance cost functions of 20 simulations of algorithms modeling rheotaxis, odor-conditioned rheotaxis (O-C Rheotaxis), and klinotaxis in the bifurcated stream based on observed data. One simulation included all 33 sea lampreys. J values with different letters are significantly different

Table 3 3kPZS increases movement activities, but water velocity is essential to direct ovulated female sea lampreys to 3kPZS source

Treatment	<i>n</i>	Leave RC	Move upstream	Enter nest	Swim past nest
3kPZS flow	51	88 % a	73 % a	47 % a	8 % a
Control flow	40	60 % b	25 % c	7 % b	13 % ab
3kPZS reduced flow	75	76 %ac	41 % b	17 % b	30 % b
Control reduced flow	38	71 % bc	13 % c	0 % b	11 % ab
<i>p</i>		0.017	<0.001	<0.001	0.075
<i>df</i>		3	3	3	3
χ^2		10.26	41.34	43.50	6.91

The number of ovulated female sea lampreys released (*n*) in the Ocqueoc River, Michigan, during differing odor and flow conditions (Treatment) and the percent females that left the release cage (leave RC), moved upstream, entered within 0.5 m² of the odorant application location (enter nest), and the percent of females that did not enter within 0.5 m² of the odorant application location, but moved at least 5 m upstream of the odorant (swim past nest). Significant differences between treatments were determined with generalized linear model assuming a binomial family. Treatments with the same letter are not significantly different ($\alpha=0.05$)

success in locating the 3kPZS source. Conversely, when exposed to the same source of 3kPZS in reduced-flow conditions, movement patterns had high degrees of sinuosity, with significantly fewer females locating the 3kPZS source. Females rarely moved upstream when no pheromone source was present, and if females did, movements were random.

Algorithm-simulated movement tracks of female sea lampreys provide additional support that odor-conditioned rheotaxis directs females to the source of 3kPZS. Rheotaxis alone (algorithm 1) did not provide sufficient control to enable simulated sea lampreys to remain in the plume and identify the location of the 3kPZS source since 3kPZS concentration was not detected. Klinotaxis (algorithm 3) did not provide consistent control to sustain the movement of females upstream due to the highly variable nature of the plume. Only simulated movements from algorithm 2, which modeled odor-conditioned rheotaxis, successfully tracked 3kPZS plumes and located 3kPZS sources. Algorithm 2 produced large-scale movements of females that were not significantly different from observed females in the bifurcated stream. Simulated female movements produced by algorithm 2 located the 3kPZS source with the same efficiency as observed females that entered the left channel. When the simulation was applied to a novel stream channel, algorithm 2 produced movements similar to observed female sea lampreys.

Although the current study demonstrates the importance of odor-conditioned rheotaxis, behavior and simulation results are not sufficient to conclude that it is the sole chemo-orientation mechanism. Stimulus source properties may have affected observed behavior and algorithm driven simulations. 3kPZS and the tracing dye were applied to the stream at a high rate (167 ml/min) through a single tube (4.8 mm diameter). This application strategy is different than the natural release of 3kPZS across the gills by male sea lampreys and may create fine scale pheromone plume artifacts. Further, 3kPZS concentration field estimates were

spatially averaged by taking large samples (cm³), whereas the odor filament sizes are likely to be an order of magnitude less. Thus, simulations lack instantaneous odor information needed to provide klinotactic comparisons. Additional studies, with a system that mimics the natural pheromone release mechanism, may reveal that odor-conditioned rheotaxis is combined with other mechanisms, such as klinotaxis (Webster et al. 2012), for sea lampreys to approach the odor source.

Odor-conditioned rheotaxis has been described in several classes of aquatic organisms at small spatial scales. At the smallest scale, odor conditioned-rheotaxis is used by microscopic marine *Nauplius* larvae of barnacle *Trevathana dentata* to locate their host, the stony reef coral *Cyphastrea chalcidicum* (Pasternak et al. 2004). Where studied in crustaceans, orientation to food odorants includes an odor-conditioned rheotaxis component to their orientation strategy, but comparisons between paired chemosensory organs also informs movements across the mean fluid flow (Page et al. 2011). Larger-scale flume experiments on fishes show that odor-conditioned rheotaxis is used by banded kokopu, eels, and smooth dogfish shark to locate food sources (Oliver et al. 1996; Baker et al. 2002; Gardiner and Atema 2007). Studies on brown bullhead (*Ameiurus nebulosus*), where successful location of a food odorant was highest in lentic environments (Sherman and Moore 2001), suggests that alternative orientation mechanisms may be present in fishes. Here we demonstrate that odor-conditioned rheotaxis may be used by sea lamprey and could be a major component of the mechanism for locating odor sources in other aquatic organisms as well.

The sea lamprey is an advantageous model for studying vertebrate chemo-orientation strategies at biologically relevant scales because they display chemo-orientation responses to a known pheromone in streams and their exquisitely sensitive olfactory system (Li et al. 1995) consists of a single naris, which precludes simultaneous comparison

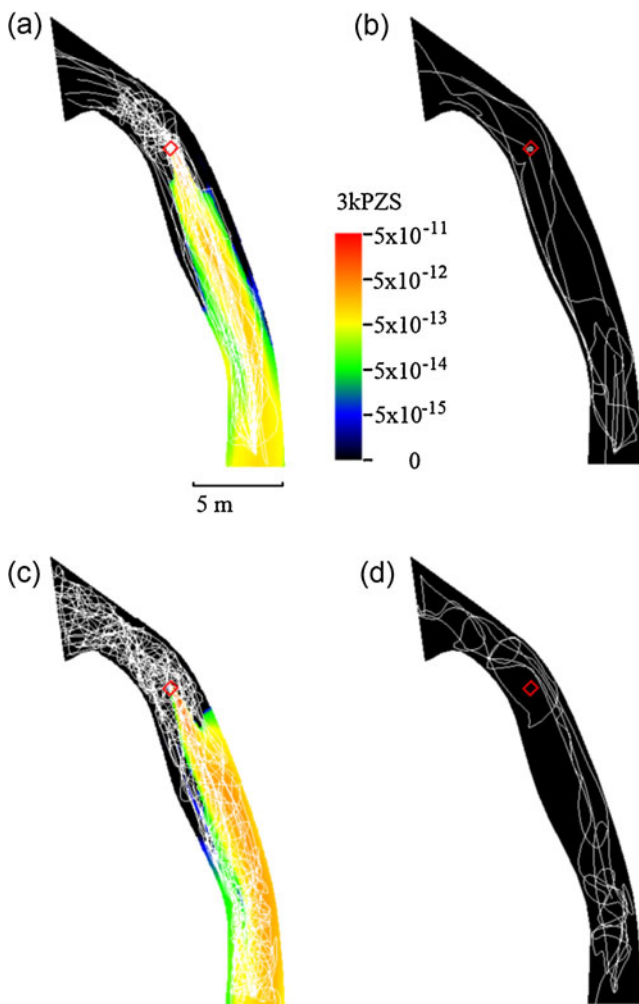


Fig. 2 3kPZS increases movement activity, but stream flow directs ovulated female sea lampreys to the 3kPZS source. Movement tracks of female sea lampreys that moved upstream of the release cage under **a** flow conditions — 3kPZS application, **b** flow conditions — control solvent application, **c** reduced-flow conditions — 3kPZS application, **d** reduced-flow conditions — control solvent application. Color coding indicates the estimated concentration of synthesized 3kPZS (M) through the stream channel. Red box is the odor application location

of odor intensity across space. River plumes are essentially one dimensional given the confines of the width and depth of the channel and the generally unidirectional fluid flow (Zimmer-Faust et al. 1995). However, when the consistency of flow direction was removed from the stream, as in reduced-flow experiments, the ability of females to track plumes of 3kPZS decreased significantly. Our results are consistent with sea lamprey reproductive ecology, where sea lamprey search for mates in lotic environments and typically do not spawn in lentic environments (Applegate 1950; Manion and Hanson 1980). Odor-conditioned rheotaxis may be especially critical to sea lamprey life history since they are not known to school during spawning migrations (Applegate 1950) and hence cannot work together with conspecifics to locate the source of pheromone, where the collective

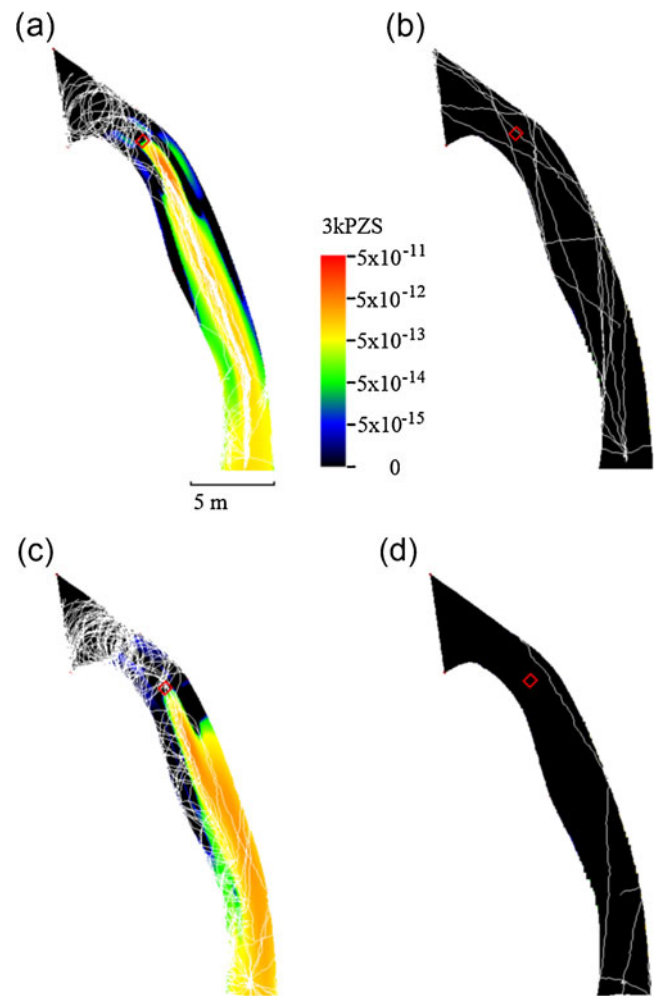


Fig. 3 Odor-conditioned rheotaxis is a robust control strategy that models observed sea lamprey behavior in novel environments. Simulated movement tracks of female sea lampreys according to algorithm modeling odor-conditioned rheotaxis in flow and reduced-flow conditions and with and without application of 3kPZS. **a** Flow conditions — 3kPZS application, **b** Flow conditions — control solvent application, **c** Reduced-flow conditions — 3kPZS application, **d** Reduced-flow conditions — control solvent application. Red box is the odor application location

schooling behavior can decipher noisy gradients for tracing the maximum point of a concentration field (Grunbaum 1998).

Table 4 Odor-conditioned rheotaxis is a robust control strategy that models observed sea lamprey behavior in novel environments

Treatment	\bar{J}	σ_J
Flow-3kPZS	3.1674	0.3644
Flow-control	2.9762	0.8751
Reduced-flow-3kPZS	4.7342	0.6351
Reduced-flow-control	3.3386	0.8372

\bar{J} and σ_J are the mean and standard deviation of the performance cost functions of 20 simulations of algorithms modeling odor-conditioned rheotaxis in differing odor and flow conditions. One simulation included all 33 sea lampreys

Engineers have formulated control algorithms based on biological descriptions of optomotor ammenotaxis, odor-conditioned rheotaxis, and chemotropotaxis to advance the prospects of programming efficient olfactory robots (Grasso et al. 1997, 2000; Li et al. 2001; Balkvosky and Shraiman 2002; Grasso and Atema 2002; Pang and Farrell 2006; Jatmiko et al. 2008). Recently, a control algorithm modeled after blue crab chemo-orientation showed an 80 % success rate at locating an odor source in turbulent flow (Webster et al. 2012). The engineered strategy used by Webster et al. (2012) was based on averaged measurements of the odorant plume, while the odor-conditioned rheotaxis algorithm present here makes a decision based on a single measurement. Given the monorhnic olfactory system of sea lamprey, the confinement of river environments, and the chemo-orientation strategy used to locate 3kPZS sources, it may be feasible to apply our algorithm to a robotic lamprey (Yu et al. 2004), and conduct field tests of the control strategy. Testing an olfactory robotic lamprey in a natural stream will eliminate uncertainty in the environmental data, account for variability in pheromone plume dynamics, while allowing the evaluation of un-modeled biological occurrences such as stopping times.

Fishes are the most diverse group of vertebrates and occupy a diverse array of environments where chemo-orientation is critical to their life history (Doving and Stabell 2003) and is accomplished through a wide array of movement patterns (Fraenkel and Gunn 1961; Jones 1968). An olfactory robot and associated algorithms would be highly versatile and able to test the role of specific sensory modalities. From an applied standpoint, use of an olfactory robotic lamprey could inform placement of pheromone-baited traps to control invasive sea lamprey in the Laurentian Great Lakes (Johnson et al. 2009) and efficiencies of different trapping strategies in various streams could be simulated prior to large capital investment in trap construction. Given that sea lamprey use odor-conditioned rheotaxis, pheromone-baited traps will be most effective where unidirectional water flow is present.

We conclude that odor-conditioned rheotaxis is an efficient chemo-orientation mechanism at much larger spatial scales than previously investigated. Our results demonstrate that this chemo-orientation mechanism is effective for a free-ranging fish to locate a synthesized pheromone source in a natural environment.

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Ethical standards Use of sea lamprey was approved under Michigan State University Institutional Animal Use and Care Committee permit 05/06-066-00. Experiments described in this manuscript comply with the current laws of the United States of America.

Conflict of interest The authors declare that they have no conflict of interest.

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